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Brain function overlaps when people observe emblems, speech, and grasping

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ABSTRACT

A hand grasping a cup or gesturing "thumbs-up", while both manual actions, have different purposes and effects. Grasping directly affects the cup, whereas gesturing "thumbs-up" has an effect through an implied verbal (symbolic) meaning. Because grasping and emblematic gestures ("emblems") are both goal-oriented hand actions, we pursued the hypothesis that observing each should evoke similar activity in neural regions implicated in processing goal-oriented hand actions. However, because emblems express symbolic meaning, observing them should also evoke activity in regions implicated in interpreting meaning, which is most commonly expressed in language. Using fMRI to test this hypothesis, we had participants watch videos of an actor performing emblems, speaking utterances matched in meaning to the emblems, and grasping objects. Our results show that lateral temporal and inferior frontal regions respond to symbolic meaning, even when it is expressed by a single hand action. In particular, we found that left inferior frontal and right lateral temporal regions are strongly engaged when people observe either emblems or speech. In contrast, we also replicate and extend previous work that implicates parietal and premotor responses in observing goal-oriented hand actions. For hand actions, we found that bilateral parietal and premotor regions are strongly engaged when people observe either emblems or grasping. These findings thus characterize converging brain responses to shared features (e.g., symbolic or manual), despite their encoding and presentation in different stimulus modalities.

1. Introduction

People regularly use their hands to communicate, whether to perform gestures that accompany speech ("co-speech gestures") or to perform gestures that – on their own – communicate specific meanings, e.g., performing a "thumbs-up" to express "it's good." These latter gestures are called "emblematic gestures" – or "emblems", and require a person to process both the action and its implied verbal (symbolic) meaning. Action observation and meaning processing are highly active areas of human neuroscience research, and significant research has examined the way that the brain processes meaning conveyed with the hands. Most of this research has focused on conventional sign language and co-speech gestures, not on emblems. Emblems differ from these other types of gesture in fundamental ways. Although individual emblems express symbolic meaning, they do not use the linguistic and combinatorial structures of sign language, which is a fully developed language system. Emblems also differ from co-speech gestures, which require accompanying speech for their meaning (McNeill, 2005). Thus, in contrast with sign language, emblems are not combinatorial and lack the linguistic structures found in human language. In contrast with co-speech gestures, emblems can directly convey meaning in the absence of speech (Ekman & Friesen, 1969; Goldin-Meadow, 1999, 2003; McNeill, 2005).

At the same time, emblems are manual actions, and as such, are visually similar to actions that are not communicative, such as manual grasping. Emblems also represent a fundamentally different way of communicating symbolic meaning compared to spoken language. Although the lips, tongue, and mouth perform actions during speech production, these movements per se neither represent nor inform the meaning of the utterance. Thus, from the biological standpoint, the brain must encode and operate on emblems in two ways, (i) as meaningful symbolic expressions, and (ii) as purposeful hand actions (Fig. 1). The ways that these two functions are encoded, integrated, and applied in understanding emblems is the subject of the present study.

Processing symbolic meaning expressed in language engages many disparate brain areas, depending on the type of language

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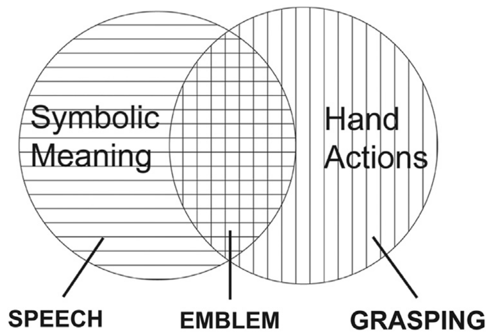

Fig. 1. Conceptual diagram of emblematic gestures (emblems). Emblems share features with speech, since both express symbolic meaning, and with grasping, since both are hand actions.

used and the goal of the communication. But some brain areas are highly replicated across these diverse communicative contexts. For example, a recent meta-analysis described semantic processing to primarily involve parts of the lateral and ventral temporal cortex, left inferior frontal gyrus, left middle and superior frontal gyri, left ventromedial prefrontal cortex, the supramarginal (SMG) and angular gyri (AG), and the posterior cingulate cortex (Binder, Desai, Graves, & Conant, 2009). More specifically, posterior middle temporal gyrus (MTGp) responses have often been associated with recognizing word meanings (Binder et al., 1997; Chao, Haxby, & Martin, 1999; Gold et al., 2006), and anterior superior temporal activity has been associated with processing combinations of words, such as phrases and sentences (Friederici, Meyer, & von Cramon, 2000; Humphries, Binder, Medler, & Liebenthal, 2006; Noppeney & Price, 2004). In the inferior frontal gyrus (IFG), pars triangularis (IFGTr) activity has often been found when people discriminate semantic meaning (Binder et al., 1997; Devlin, Matthews, & Rushworth, 2003; Friederici, Opitz, & Cramon, 2000), while pars opercularis (IFGOp) function has been linked with a number of tasks. Some of these tasks involve audiovisual speech perception (Broca, 1861; Hasson, Skipper, Nusbaum, & Small, 2007; Miller & D'Esposito, 2005), but others involve recognizing hand actions (Binkofski & Buccino, 2004; Rizzolatti & Craighero, 2004).

Prior biological work on the understanding of observed hand actions implicates parietal and premotor cortices. In the macaque, parts of these regions interact to form a putative "mirror system" that is thought to be integral in action observation and execution (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Fogassi, Gallese, Fadiga, & Rizzolatti, 1998; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). A similar system appears to be present in humans, and also to mediate human action understanding (Fabbri-Destro & Rizzolatti, 2008; Rizzolatti & Arbib, 1998; Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001). Studies investigating human action understanding have, in fact, found activity in a variety of parietal and premotor regions when people observe hand actions. This includes object-directed actions, such as grasping (Buccino et al., 2001; Grezes, Armony, Rowe, & Passingham, 2003; Shmuelof & Zohary, 2005, 2006), and non-object-directed actions, such as pantomimes (Buccino et al., 2001; Decety et al., 1997; Grezes et al., 2003). More precisely, some of the parietal regions involved in these circuits include the intraparietal sulcus (IPS) (Buccino et al., 2001, 2004; Grezes et al., 2003; Shmuelof & Zohary, 2005, 2006) and inferior and superior parietal lobules (Buccino et al., 2004; Perani et al., 2001; Shmuelof & Zohary, 2005, 2006). In the premotor cortex, this includes the ventral (PMv) and dorsal (PMd) segments (Buccino et al., 2001; Grezes et al., 2003; Shmuelof & Zohary, 2005, 2006). Because emblems are hand actions, perceiving them should also involve responses in these areas. However, it remains an open question the extent to which these areas are involved in emblem processing. Further, the anatomical and physiological mechanisms used by the brain to decode the integrated manual and symbolic features of emblematic gestures are not known.

Recently, an increasing number of studies have sought to understand the way that the brain gleans meaning from manual gestures, particularly co-speech gestures. In general, co-speech gestures appear to activate parietal and premotor regions (Kircher et al., 2009; Skipper, Goldin-Meadow, Nusbaum, & Small, 2009; Villarreal et al., 2008; Willems, Ozyurek, & Hagoort, 2007). Yet, activity during co-speech gesture processing has also been found in regions associated with symbolic meaning (see Binder et al., 2009 for review). These regions include parts of the IFG, such as the IFGTr (Dick, Goldin-Meadow, Hasson, Skipper, & Small, 2009; Skipper et al., 2009; Willems et al., 2007) and lateral temporal areas, such as the MTGp (Green et al., 2009; Kircher et al., 2009).

It is not surprising that areas that respond when people comprehend language also respond when people comprehend gestures in the presence of spoken language. Several studies thus attempt to disentangle the brain responses specific to the meaning of co-speech gestures from those of the accompanying language. Typically, this is done by contrasting audiovisual speech containing gestures with audiovisual speech without gestures (Green et al., 2009; Willems et al., 2007). By way of subtractive analyses, the results generally reflect greater activity in these "language" areas when gestures accompany speech than when they don't. Greater activity in these areas is then taken as a measure of their importance in determining meaning (Skipper et al., 2009; Willems et al., 2007).

However, co-speech gestures are processed interactively with accompanying speech (Bernardis & Gentilucci, 2006; Gentilucci, Bernardis, Crisi, & Dalla Volta, 2006; Kelly, Barr, Church, & Lynch, 1999), and it is the accompanying speech that gives co-speech gestures their meaning (McNeill, 2005). In other words, speech and gesture information do not simply add up in a linear way. Thus, when the hands express symbolic information, it is difficult to truly separate the brain responses attributable to gestural meaning from those of the accompanying spoken language.

Previous research to examine brain responses to emblems does not present a clear profile of activity that characterizes how the brain comprehends them. This may be due partly to the wide variation in methods and task demands in these studies. Indeed, prior emblem research has been tailored to address such diverse questions as their social relevance (Knutson, McClellan, & Grafman, 2008; Lotze et al., 2006; Montgomery, Isenberg, & Haxby, 2007; Straube, Green, Jansen, Chatterjee, & Kircher, 2010), emotional salience (Knutson et al., 2008; Lotze et al., 2006), or shared symbolic basis with pantomimes and speech (Xu, Gannon, Emmorey, Smith, & Braun, 2009). Accordingly, the results implicate a disparate range of brain areas. These areas include the left IFG (Lindenberg, Uhlig, Scherfeld, Schlaug, & Seitz, 2012; Xu et al., 2009), right IFG (Lindenberg et al., 2012; Villarreal et al., 2008), insula (Montgomery et al., 2007), premotor cortex (Lindenberg et al., 2012; Montgomery et al., 2007; Villarreal et al., 2008), MTG (Lindenberg et al., 2012; Villarreal et al., 2008; Xu et al., 2009), right (Xu et al., 2009) and bilateral fusiform gyri (Villarreal et al., 2008), left (Lotze et al., 2006) and bilateral inferior parietal lobules (Montgomery et al., 2007; Villarreal et al., 2008), medial prefrontal cortex (Lotze et al., 2006; Montgomery et al., 2007), as well as the temporal poles (Lotze et al., 2006; Montgomery et al., 2007). This represents a very large set of brain responses to emblems and does not clarify the question of interest here, namely the mechanisms underlying the decoding of symbolic and manual information.

In the present study, we aimed (1) to identify brain areas that decode symbolic meaning, independent of its expression as emblem or speech, and (2) to identify brain areas that process hand actions, regardless of whether they are symbolic emblems or non-symbolic grasping actions. To identify brain areas sensitive to symbolic meaning, we had participants watch an actor communicate similar meanings with speech (e.g., saying "It's good") and with emblems